

REHASHING BUSHMEAT – INTERVIEW CAMPAIGNS REVEAL SOME CONTROVERSIAL ISSUES ABOUT THE BUSHMEAT TRADE DYNAMICS IN NIGERIA

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RÉSUMÉ.— *La viande de brousse : des enquêtes révèlent des points de controverse sur la dynamique de son commerce au Nigéria.*— Sur la base d'enquêtes dans le sud du Nigéria, cet article examine (i) si la viande de brousse est toujours une source cruciale de protéines pour les communautés locales, (ii) si elle est toujours culturellement bien justifiée et (iii) si, selon les préférences des consommateurs, des valeurs différentes sont attribuées aux divers types d'espèces constituant cette viande de brousse. De plus, cet article fournit des informations sur la question de savoir (iv) si le commerce de la viande de brousse épuise localement les populations des espèces ciblées, et (v) si la disparition sur les marchés de grands animaux est signe de leur extermination locale. Une combinaison d'entretiens avec des hommes et des femmes de différentes classes d'âge, incluant des chasseurs, consommateurs et vendeurs, a été conduite dans divers localités nigérianes correspondant à différentes conditions d'habitat et de caractéristiques socio-économiques et ethniques. Les résultats suggèrent que la consommation de viande de brousse, en particulier dans les zones urbaines, n'a pas une grande valeur de subsistance, sauf pour une petite sous-section de la communauté. De fait, même dans les zones rurales, moins de 30 % des personnes de moins de 50 ans interrogées ont répondu consommer fréquemment de la viande de brousse. L'importance culturelle de la viande de brousse a substantiellement diminué dans les années récentes, comme en témoigne le fait que (i) cette source de nourriture a été rapidement abandonnée durant la crise d'Ebola en 2014 et (ii) la plupart des personnes interrogées ont affirmé n'en manger que rarement voire pas du tout. Les données recueillies vont dans le sens de ce que le prix d'une carcasse serait principalement déterminé par la taille de l'animal et non pas par la préférence des consommateurs. L'utilisation et le commerce de la viande de brousse peuvent certainement épuiser localement les populations des espèces animales ciblées. Néanmoins, il n'y a toujours pas suffisamment de preuves empiriques de la notion selon laquelle quand les grands animaux disparaissent des marchés cela signifierait que leurs populations auraient été considérablement épuisées voire exterminées. De fait, sur la base d'éléments culturels exposés par les chasseurs interrogés, il semblerait que cette notion soit erronée, du moins en ce qui concerne les régions ouest-africaines les plus riches et les plus économiquement dynamiques. Il est conseillé à ceux qui étudient la viande de brousse d'explorer plus en profondeur la flexibilité culturelle des communautés humaines avant de généraliser des conclusions, évitant ainsi d'extrapoler à grande échelle des conclusions insuffisamment fondées car basées sur des données collectées à très petite échelle spatiale et durant de courtes périodes de temps.

SUMMARY.— Using questionnaire surveys in southern Nigeria, this paper explores whether: (i) bushmeat is still a crucial source of animal protein for local communities; (ii) is still culturally very relevant; and (iii) if people value differently the various kinds of bushmeat species because of customer preferences. In addition, this paper provides information on whether (iv) the bushmeat trade locally depletes target game species; and (v) whether the disappearance of large animals from the markets would indicate their local extirpation from the wild. A combination of interviews was carried out with both men and women of different age classes including hunters, consumers and sellers, from different Nigerian locations with different habitat conditions, socio-economic and ethnic characteristics. Results of these interviews suggest that the consumption of bushmeat has little subsistence value, especially in urban areas, except for a small sub-section of the community. Indeed, even in rural areas less than 30 % of the interviewees of less than 50 years age answered that they frequently eat bushmeat. Cultural importance of bushmeat decreased substantially in recent years, as shown by that (i) this food source was quickly abandoned by people during the 2014 Ebola crisis, and (ii) most of questionnaire respondents affirmed that they

would have eaten bushmeat only rarely or even not at all. There was support for the notion that the price of a carcass was mainly determined by the animal size and not by the consumer preference. Bushmeat utilization and trade may certainly deplete target animal species at the local scale. Nonetheless, there is still no sufficient empirical evidence for the notion that, when large animals disappeared from the markets, it meant that their populations were heavily depleted or even extinct. Indeed, based on cultural elements highlighted by interviewed hunters, there is evidence that this notion may be wrong, at least in the richest and economically more dynamic regions of West Africa. It is advised that bushmeat studies should explore more in depth the cultural flexibility of human communities before drawing generalized conclusions, thus avoiding unsupported large-scale conclusions based on data collected at a very small spatial scale and during short time periods.

The use and exploitation of bushmeat for tradition and subsistence has received considerable scientific attention in Central and West Africa (e.g., Ajayi, 1978; Fa *et al.*, 2006; Kiffner *et al.*, 2015), being currently one of the main research fields in tropical conservation biology. Indeed, a Google search (made on 09 June 2016) with ‘bushmeat trade’ as keywords revealed a total of 303 000 pages, thus showing the great attention of media towards this subject.

The large body of published studies focused on the multiple factors that affect bushmeat exploitation, including socio-economic contexts, availability of alternative sources of protein, ethnicity, availability of bushmeat (e.g., Fa *et al.*, 2003, 2015; Kiffner *et al.*, 2015), ecological aspects (e.g., Petrozzi *et al.*, 2016) and conservation implications (e.g., Fa *et al.*, 2015). These studies generated a plethora of rules/assumptions/predictions that were in turn generalized to multiple contexts in Africa and elsewhere.

During two decades (1996-2015) of bushmeat markets monitoring and ecological investigations in West Africa (particularly in southern Nigeria and Togo; see Luiselli *et al.*, 2013; Akani *et al.*, 2015; Petrozzi *et al.*, 2015), the authors of the present note collected field data and interviews that may partially challenge some acclaimed interpretations generated by earlier studies. Our data on the controversial issues of bushmeat exploitation and trade were collected mostly opportunistically (i.e. at irregular time intervals, with different field efforts between sites, and with a small number of interviews) or are based on studies performed at the local scale, thus making generalizations difficult. However, the same is true for many other research papers published on the subject (e.g., East *et al.*, 2005; Schulte-Herbrüggen *et al.*, 2015).

In this paper, using southern Nigeria as a case of study, we analyse the following issues:

- (1) Bushmeat is a crucial source of animal protein for West and Central African human communities (e.g., Ntiamoa-Baidu, 1995; Fa *et al.*, 2000; Bashares *et al.*, 2011; Foerster *et al.*, 2011).
- (2) Bushmeat is culturally very relevant for human communities (Fa *et al.*, 2002a, 2002b; Cronin *et al.*, 2015). Cultural aspects are more important than economic correlates in explaining bushmeat consumption and preference in Amazonia (Morsello *et al.*, 2015), thus the same may apply to our geographic context as well.
- (3) People value differently the various kinds of bushmeat species because of customer preferences (Schenck *et al.*, 2006; Wright & Priston, 2010).
- (4) Bushmeat trade locally depletes target species and communities (Rowcliffe *et al.*, 2003; Cowlishaw *et al.*, 2005; Fa & Brown, 2009; Abernethy *et al.*, 2013; Grande-Vega *et al.*, 2016).
- (5) Disappearance of large animals (apes, buffaloes, elephants, big cats, large crocodiles, etc.) from the bushmeat markets would indicate heavy depletion or even extirpation of their populations (Nasi *et al.*, 2011; Dupain *et al.*, 2012).

Based on the above-mentioned issues, we specifically answer to the following key questions:

- (1) Is bushmeat still a crucial source of animal protein? This question is central because wide areas of West Africa are economically blooming and under rampant urbanization (Corral *et al.*,

2015), and least people should rely on bushmeat for their subsistence compared to a few decades ago.

(2) Does bushmeat still keep a deep cultural relevance for people? As many aspects of ‘rural life’ are changing in the rapidly evolving economies and societies of West Africa (Deininger, 2003; Binswanger-Mkhize & McCalla, 2008; Corral *et al.*, 2015), a modification of the cultural issues linked to the bushmeat consumption may be possible.

(3) Do people still value differently the various kinds of bushmeat species because of customer preferences or are all types of traded wild animals ‘just bushmeat’? Indeed, customer preferences for bushmeat may shift in rapidly developing countries (e.g., Kuhnlein & Receveur, 1996; Warde, 1997) being influenced by a more urbanized, globalized and Western-World-like economy and life style (Sabater-Pi & Groves, 1972; East *et al.*, 2005).

(4) Does bushmeat trade locally deplete target species and communities?

(5) When large animals disappear from the markets, does it necessarily mean that their populations were much depleted or extirpated?

We answer to the above key questions by using original bushmeat market data and especially structured interviews carried out in southern Nigeria. These interviews were done with both men and women of different ethnic origin and age classes, including hunters, consumers and sellers, recruited from different places with varied natural and socio-economic environments. Our aims are not to criticize or contradict earlier studies, but to furnish novel ways of interpretation for potentially controversial issues in this research field.

MATERIALS AND METHODS

STUDY AREA

Field data were collected in southern Nigeria (Delta, Edo, Bayelsa, Rivers, Akwa-Ibom, Cross River states; Fig. 1).



Figure 1.— Map of Nigeria, showing the surveyed areas in the Delta, Edo, Bayelsa, Rivers, Akwa-Ibom, Cross River states. 1 = Edo State, 2 = Delta State, 3 = Bayelsa State, 4 = Rivers State, 5 = Akwa-Ibom State, 6 = Cross River State.

This area is characterized by an alternation of mangrove and swamp forest patches across a wide mosaic of farms and urban centres (Luiselli *et al.*, 2015). The study area is among the most industrialized and developed of the whole African continent, and houses huge petrochemical installations (De Montclos, 1994; UK DFID, 2015). It is also one of the regions of Africa with highest human population density (UK DFID, 2015). Importantly for our study, this area underwent a tremendous economic growth during the past twenty years, with Nigeria being now the first economy of the African continent (UK DFID, 2015). During this development process, there has been a massive immigration of formerly rural

families into metropolitan areas, with a substantial reduction of poverty also in rural areas due to revenues of money transferred from people in the metropolitan area towards their relatives living in the villages (Corral *et al.*, 2015).

PROTOCOL

Field data were collected between 1996 and 2015. During 1996-2011, general data on traded species and market dynamics were recorded opportunistically, while surveying bushmeat markets for studies focused on the ecology and conservation of reptiles (e.g., Akani *et al.*, 1999; Luiselli, 2003a, 2003b; Luiselli *et al.*, 2013, 2016). During this ‘opportunistic phase’ of our studies, we made over 500 non-structured oral interviews with hunters (asking about their target preys and the habitat/locality of their hunting activities, the reasons beyond their selection of a given prey type, and their selling prices and income, age, place of residence, and ethnicity), and also recorded data on charismatic species traded in the market (large mammals, primates, large birds).

In 2011-2015, ten markets (Tab. I) were visited regularly (at least once per month), with all carcasses sold being recorded and the hunters/traders being interviewed (Luiselli *et al.*, 2013; Akani *et al.*, 2015a, 2015b; Petrozzi *et al.*, 2015). These markets were also explored during 2014 in order to assess the effects of the Ebola crisis on the bushmeat trade (Akani *et al.*, 2015c).

TABLE I

Name-place and geographic coordinates of the bushmeat markets that were regularly surveyed in 2011-2015

Site	State	Latitude	Longitude
Swali	Bayelsa	04°55'N	06°17'E
Mosogar	Delta	05°54'N	05°43'E
Patani	Delta	05°13'N	06°11'E
Aduwawa (Oredo)	Edo	06°22'N	05°41'E
Imo River Bridge	Rivers	04°53'32"N	07°10'E
Omagwa	Rivers	04°59'04"N	06°55'05"E
Akabuka	Rivers	05°12'36"N	06°38'22"E
Ahohada	Rivers	05°04'58"N	06°39'30"E
Mbiama	Rivers	05°03'N	06°27'E
Eket Bridge	Akwa-Ibom	04°38'48"N	07°56'34"E

During the year 2012 (i.e. before the Ebola crisis in West Africa), interview campaigns with randomly encountered people were performed in order to understand patterns and trends of bushmeat consumption across the study region. All interviews were performed by local researchers, in order to minimize the potential biases due to fear of respondents (Fav *et al.*, 2010; Knapp *et al.*, 2010; St. John *et al.*, 2010, 2011; Keane *et al.*, 2011; Jenkins *et al.*, 2011; Moro *et al.*, 2013). Randomly encountered people were interviewed in both urban areas (Port Harcourt metropolitan area, Rivers State; > 5 million people) and in rural areas (41 different villages in the Niger Delta, each one with a population < 5,000 people, interspersed in the forest-plantation mosaic habitat). Gender, age (three categories: (a) ≤ 25 years, (b) 26-50 years, (c) ≥ 51 years), and schooling degree of all interviewees were recorded. Names of the interviewees were not recorded to minimize disturbance to people’s privacy (St. John, 2010; Nuno *et al.*, 2014). People were randomly recruited in the typical places of their routine activities (Tab. II). Interviewees were asked the following two questions: (1) do you like eating bushmeat? (2) if yes, how often do you eat it? Interviewees were offered the possibility to choose whether they use to eat bushmeat frequently (at least 1 time per week), rarely (about once per month or less) or never. Those respondents answering that they would eat at least occasionally bushmeat were asked to indicate whether they would select the type of animal to eat (a) always, (b) often, or (c) never, i.e. thus buying/eating what is available.

The total interviewed sample consisted of 421 men (242 in urban and 179 in rural areas) and 325 women (212 in urban and 113 in rural areas) (Tab. II). In rural areas, we interviewed a mean of 4.37 men and 2.76 women per village. Age ranged from 16 to 82 years in men, and from 18 and 87 years in women.

STATISTICAL ANALYSES

All variables were tested for normality (Kolmogorov-Smirnov test) and collinearity (Pearson’s correlation coefficient) before being entered into any analysis. Schooling degree was negatively collinear with age classes ($r = -0.98$, $n = 3$, $P = 0.027$), with highest levels of schooling in people ≤ 25 years and lowest levels of schooling in people ≥ 51 years). Thus, schooling degree was deleted from any further analyses.

Chi-square test was used to examine differences in the frequencies of responses about bushmeat consumption between groups from different villages, age classes and gender.

Two independent Generalized Linear Models (GLZs) were used to model the interview results on the bushmeat consumption and to quantify the distribution of different types of answer in relationship with site (rural versus urban), gender (men versus women) and age classes (three categories) (Hosmer & Lemeshow, 2000). As dependent variables, in

the first model all the results of systematic interviews (sample size for each type of answer), and in the second model the sample size for the response “never eating bushmeat” were used. In both GLZs, the identity link function and a normal distribution of error were used (McCullagh & Nelder, 1989). A stepwise forward regression procedure was used to test the statistical significance of each variable in turn, and variables were excluded when they did not correlate significantly to the dependent variable (Wald test $P > 0.05$). The significant variables were computed using the best subset procedure.

In order to explore deviance and hierarchical partitioning, the selected variables were analysed in order to determine the comparative influence of each variable (Borcard *et al.*, 1992). The decomposition of the variation into subsets of explanatory variables was carried out by means of a partial regression analysis (Legendre & Legendre, 1998).

Alpha level was set at 5 %. All tests were performed with Statistica version 6.0 software.

TABLE II

Distribution of interviewees by age, gender (M = Men, W = Women), rural versus urban areas, in relation to the precise places where they were interviewed

	Men (years) (TOTAL)	M ≤ 25	M 26-50	M ≥ 51	Women (years) (TOTAL)	W ≤ 25	W 26-50	W ≥ 51
URBAN AREAS								
Mall	30	10	10	10	32	12	10	10
Hotel	29	11	11	7	21	12	6	3
Canteen	21	5	8	8	23	7	8	8
Restaurant	25	8	10	7	14	6	4	4
Market	45	15	15	15	42	10	18	14
Hair-making saloon	13	7	3	3	40	20	12	8
Food shop	37	10	10	17	26	8	12	6
Walking/selling on road	42	14	14	14	14	2	7	5
Total	242	80	81	81	212	77	77	58
RURAL AREAS								
Canteen	21	7	7	7	11	5	6	0
Market	40	15	15	10	41	9	17	15
Hair-making saloon	2	2	0	0	23	13	7	3
Food shop	11	2	5	4	14	3	6	5
Walking/selling on road	35	14	11	10	6	2	2	2
Farming	36	8	23	5	18	2	14	2
Hunting	34	12	12	10	0	0	0	0
Total	179	60	73	46	113	34	52	27

RESULTS AND DISCUSSION

In the following text headings, first we define the general issues in terms of research question, second we summarize the main literature on the subject, and third we discuss our original data and points of view that may eventually challenge them.

IS BUSHMEAT STILL A CRUCIAL SOURCE OF ANIMAL PROTEIN FOR LOCAL COMMUNITIES?

The use of wildlife proteins was considered to be very important and often the first source of protein for local communities in different African countries (Chardonnet *et al.*, 1995; Ntiemoa-Baidu, 1995; Fa *et al.*, 2000, 2003, 2015; Pinstrip-Andersen *et al.*, 2001; Bakarr *et al.*, 2002; Williamson, 2002; Milner-Gulland & Bennett, 2003; Starkey, 2004; Nasi *et al.*, 2008; Bashares *et al.*, 2011; Foerster *et al.*, 2011). Protein derived from wild animals accounted for 30 to 90 % of total animal protein (Olatunbosun *et al.*, 1972; Ajayi, 1978, 1979; de Vos, 1978; Prescott-Allen & Prescott-Allen, 1982; Asibey, 1987; Hladik, 1987; Koppert *et al.*, 1996). Nonetheless, many of the studies supporting the notion that bushmeat is a primary source of protein for people are relatively old (e.g., Olatunbosun *et al.*, 1972; Ajayi, 1978; Prescott-Allen & Prescott-Allen, 1982; Asibey, 1987; Hladik, 1987). Nowadays, although there are some zones in rural West Africa where bushmeat may still supply a considerable portion of the needed animal proteins (Cawthorn & Hoffman, 2015), we doubt that the above-mentioned estimates can be generalized. For instance, Akani *et al.* (2015c) showed that the number of traded carcasses (and consequently also the

economical turnover of bushmeat trade) collapsed quickly in nine markets of southern Nigeria soon after the Federal Government proclaimed the national emergency for the Ebola crisis and used media (radio, television, newspaper) campaigns to advise people to avoid consumption of bushmeat (Akani *et al.*, 2015c). The extremely prompt response of people towards the avoidance of eating bushmeat is, in our opinion, a clear evidence that very few, if any, people in southern Nigeria still rely on bushmeat to survive. The same pattern also occurred in Ivory Coast (Sery Gonedele Bi, unpublished data) and Burkina Faso (Emmanuel Hema, unpublished data), thus confirming that the findings by Akani *et al.* (2015c) were not at all an isolated circumstance and may be generalized to large sectors of West Africa.

Our systematic interviews revealed significant differences in people's type of answers between rural and urban areas and between sexes ($\chi^2 = 97$, $df = 2$, $P < 0.001$; Tab. III). There were significantly higher frequencies of interviewees reporting to consume bushmeat in rural areas (Fig. 2). The great majority of urban people answered that they would not eat bushmeat at all or very rarely. This was especially true for young people (≤ 25 years age) (Tab. III). In contrast with earlier literature (Cawthorn & Hoffman, 2015), men answered that they would 'often' eat bushmeat significantly more ($P < 0.05$) than women irrespective of age class (Fig. 2). Older people (≥ 51 years age) also answered that they would 'often' eat bushmeat significantly more than younger people (≤ 25 years) also in rural areas ($P < 0.05$ at χ^2 test; Tab. III). This latter pattern mirrors earlier literature (Cawthorn & Hoffman, 2015).

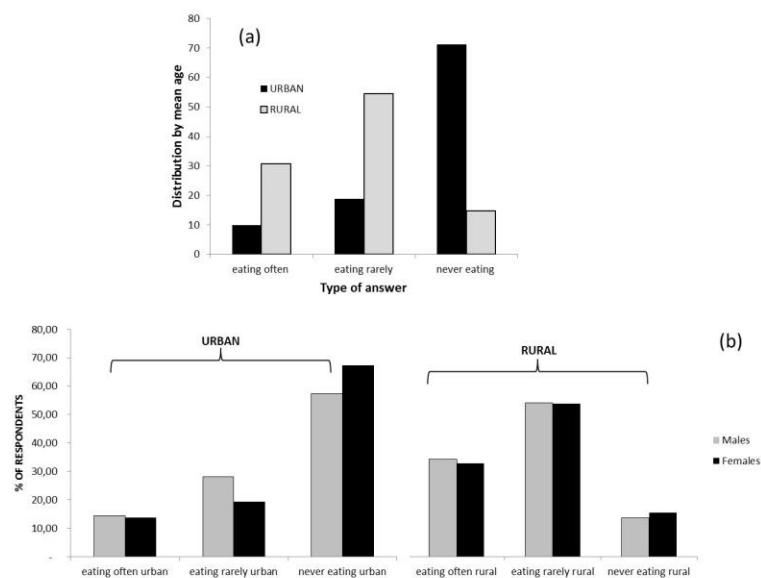


Figure 2.— Distribution of the mean percentages of the ages of the interviewed people (men and women pooled) divided by rural/urban area (graphic (a)) and by sex (graphic (b)), in southern Nigeria. People were asked to answer to the question: 'do you like eating bushmeat and how often do you eat it?'.

A first GLZ model, inclusive of all the types of answers by interviewees, revealed remarkable variation between rural and urban areas and between sexes (Tab. IV). In this model, the relative importance of predictors (pure effect), as determined by hierarchical partitioning, showed that

rural versus urban environment was the most important variable (39.5 % of explained variance), followed by sex, whereas age explained a very low percentage of variance (Fig. 3).

TABLE III

Synoptic table of the interviewees' responses to the question 'do you like eating bushmeat and how often do you eat it? ', delivered to randomly encountered people in the Niger Delta (southern Nigeria). The data are entered by sex and age class

	Urban			Rural			Total
	eating often	eating rarely	never eating	eating often	eating rarely	never eating	
Men (≤ 25 yr)	7	14	56	17	31	11	136
Men (26-50 yr)	12	23	44	21	23	8	131
Men (≥ 51)	16	31	39	22	41	5	154
Total Men	35	68	139	60	95	24	421
Women (≤ 25 yr)	3	6	62	13	43	14	141
Women (26-50 yr)	7	12	46	9	11	2	87
Women (≥ 51)	19	23	35	14	5	1	97
Total Women	29	41	143	36	59	17	325
TOTAL SAMPLE	64	109	282	96	154	41	

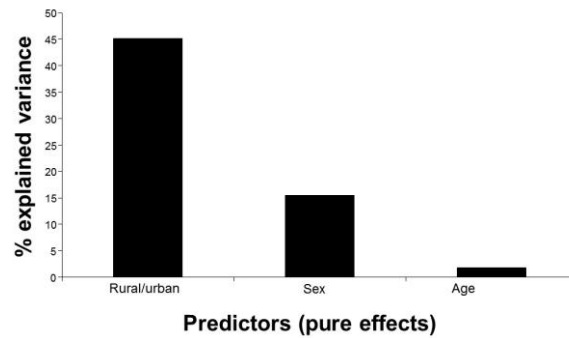


Figure 3.— Relative importance of predictors (pure effect), as determined by hierarchical variation partitioning, for the model considering all the interviewees' responses as dependent variable.

A second GLZ model, inclusive of only 'never eating' answers, revealed significant differences between rural and urban areas and among age classes (Tab. IV). Thus, this model showed that the probability of finding people who had never eaten bushmeat increased in the urban environment and was inversely related to age. In terms of hierarchical partitioning of variance, our analysis showed that the stronger pure effect was accounted for the urban versus rural area (88 % of explained variance), followed by age classes, while the gender accounted only for an extremely low percent of explained variance (Fig. 4).

TABLE IV

Results of Generalized Linear Model (GLZ) estimates showing: i) significant differences in the types of answers by interviewees (rural and urban areas and sex) and ii) significant relationship between urban and rural and age classes in bushmeat consumption (expressed in terms of numbers of interviewees admitting that they do not eat bushmeat)

Variable	Estimate	Standard Error	Wald	P
<i>All interviewees' responses included</i>				
Intercept	40.5	6.5	40	< 0.00001
Sex	16	7.39	4.6	0.030478
Urban vs. rural	27.33	7.39	13.66	0.000219
<i>Only 'never eat bushmeat' responses included</i>				
Intercept	810.08	131.16	38.15	< 0.00001
Age	-7.88	1.29	37.51	< 0.00001
Urban vs. rural	40.17	2.10	365.96	< 0.00001

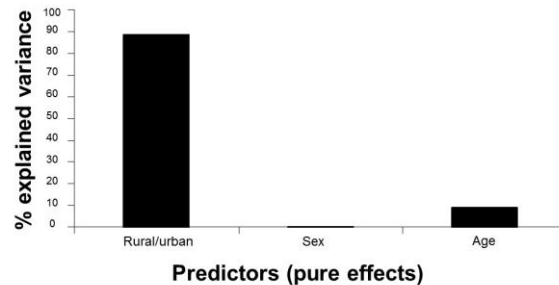


Figure 4.— Relative importance of predictors (pure effect) as determined by hierarchical variation partitioning for the model including only the ‘never eat bushmeat’ responses.

The Nigerian patterns are very clear: the consumption of bushmeat is of little significance in urban areas, with only a minority of the population (< 8%) reporting that they consumed it often, whereas it can still be of some relevance in rural areas. However, even in rural areas, bushmeat was frequently consumed by less than 30 % of the interviewees of less than 50 years age, thus strongly suggesting that it could not have a true subsistence role for people. Mirroring our interview data, it should be stressed that the consumption of poultry has grown tremendously in West Africa during the last decades (global poultry trends reported from FAO, 2013). We suggest that the supplies of poultry meat may have substituted bushmeat as a subsistence protein source for people, at least in very wide parts of West Africa.

DOES BUSHMEAT STILL KEEP A DEEP CULTURAL RELEVANCE FOR PEOPLE?

There is ample consensus on the notion that bushmeat consumption is an important cultural element for West African people, with subsistence hunting, commercial hunting and hunting for cultural reasons (not directly linked to subsistence) often cohabiting in a same region of West Africa (e.g., Asibey & Child, 1991; Wilkie & Carpenter, 1999; Bowen-Jones *et al.*, 2002; Van Vliet & Mbazza, 2011). Subsistence hunting typically occurs at the level of the local scale in rural areas, and often involves small sized animals such as rodents, bats, etc. On the other hand, commercial hunting supplies a luxury market, dictated by cultural reasons in the urban areas (Asibey & Child, 1991), with wealthy and middle-class people being the main consumers (Fa *et al.*, 2002). Commercial hunting persists due to the still surviving links between the urban consumers and their geographic origin (Schenck *et al.*, 2006; Willcox & Nambu, 2007), including also religious belief (Fa *et al.*, 2002a, 2002b; East *et al.*, 2005; Cronin *et al.*, 2015). In addition, bushmeat may have some ‘magic’ connotations, at least in remote villages. For instance, in the villages of Boje and Nsadop (northern Cross River State, Nigeria) the palm civet (*Nandinia binotata*) is consumed as a ju-ju food before fights or local wars because it is considered to favour good luck during combats (Amadi *et al.*, 2015).

Although bushmeat undoubtedly retains a deep cultural relevance for local communities in many areas of West Africa, we suggest that its cultural importance has been nowadays decreasing substantially in the economically wealthier and more developed areas such as southern Nigeria. Indeed, the fact that (i) this food source was quickly abandoned during the Ebola crisis (Akani *et al.*, 2015c) and that (ii) most of our interviewees answered that they would eat bushmeat only rarely or even not at all (Fig. 2), should indicate a currently moderate cultural weight of eating bushmeat in southern Nigeria.

ISN'T BUSHMEAT JUST BUSHMEAT? THAT IS: DO PEOPLE VALUE DIFFERENTLY THE DIFFERENT KINDS OF ANIMALS?

Intuitively, preference for its taste compared to commercial meat has often been considered as a main reason for buying bushmeat, in such different cultural contexts as in Gabon (Schenck *et al.*, 2006), Cameroon (Njiforti, 1996; Wright & Priston, 2010), and Ghana (Falconer, 1992; Ntiama-Baidu, 1992). Falconer (1992) and Ntiama-Baidu (1992) argued that price can vary remarkably across bushmeat species because of their intrinsic value (i.e. taste) and independently on the weight of the sold meat. These results were confirmed by other studies (e.g., Fa *et al.*, 2000; MacDonald *et al.*, 2011; Van Vliet *et al.*, 2012), suggesting that selective harvesting can indicate that hunters catch species according to the preference of the consumers (Wright & Priston, 2010). However, in rural markets of Cameroon price increased approximately as a function of the square root of carcass mass while in urban markets price increased more dramatically as size increased than in rural markets (MacDonald *et al.*, 2011). Therefore, in this latter study the price of a carcass was mainly determined by the animal size, as also found in another African study (Wilkie & Godoy, 2001).

The same trend observed by Wilkie & Godoy (2001) and MacDonald *et al.* (2011) was detected by us in the Swali market of Bayelsa State, Niger Delta, Nigeria (dataset available in Akani *et al.*, 2015a). We observed that there was a highly linearly positive relationship between mean weight of the sold carcass and its prize ($r = 0.940$, $n = 13$ animal species, $P < 0.001$), thus showing that in terms of economic value, the size of the animal determined almost entirely the price (Akani *et al.*, 2015a).

Our interview data (Tab. V) showed that, in urban areas there were significant differences among age classes (χ^2 test with $df = 2$, $P < 0.05$) in terms of frequency of the three types of answers (i.e., 'always select', or 'often select', or 'never select' the type of bushmeat to eat), with significantly fewer young people (≤ 25 years) being unselective. There were no intersexual significant differences in this pattern (χ^2 test with $df = 1$, $P > 0.05$). Also in rural areas there were significant differences among age classes in terms of frequencies of the three types of answers (χ^2 test with $df = 2$, $P < 0.05$), with a significantly higher frequency of old people (≥ 51 years) being unselective (Tab. V). Also in this case, there were no significant differences between sexes (χ^2 test with $df = 1$, $P > 0.05$). Overall, most of the interviewees answered that they would eat whatever bushmeat type is available, apart from young urban people of both sexes. These latter usually do not eat bushmeat (Tab. III) but, when they do, are selective in the type of animal eaten (Tab. V).

TABLE V

Synoptic table of the interviewees' responses on whether (a) they would select the type of animal to eat (a) always, (b) often, or (c) just buying/eating what is available, delivered to randomly encountered people in the Niger Delta (southern Nigeria). The data are entered by sex (M = Men, W = Women) and age class (in years)

	M (Total)	M (≤ 25 yr)	M (26-50 yr)	M (≥ 51 yr)	W (Total)	W (≤ 25 yr)	W (26-50 yr)	W (≥ 51 yr)
Urban areas								
Total	103	21	35	47	70	9	19	42
Always selecting the type of animal	37	18	13	6	18	9	6	3
Often selecting the type of animal	32	2	18	12	26	0	7	19
Just buying/eating what is available	34	1	4	29	26	0	6	20
Rural areas								
Total	155	48	44	63	95	56	20	19
Always selecting the type of animal	18	7	8	3	14	8	2	4
Often selecting the type of animal	86	23	18	45	36	23	6	7
Just buying what is available	51	18	18	15	45	25	12	8

Our hypothesis to explain the above patterns is that, in southern Nigeria, year-by-year the bushmeat is becoming more and more 'just bushmeat', with a loss of the intrinsic value of the different kinds of meat. In other words, in a country where the economy is growing quickly and

lesser people are directly involved for subsistence by rural life-style (Corral *et al.*, 2015), bushmeat (with little difference among the various kinds of animals) just represent a trendy alternative to the usual commercial meat (poultry, beef, goat and pork). Indeed, the economic growth of Nigeria has been tremendous over the last 20 years, with the country being currently ranked as the 21st largest economy in the world in terms of nominal GDP, the 20th largest in terms of Purchasing Power Parity and the 1st economy of Africa (UK DFID, 2015). The urban middle class, without subsistence problems and scarcely connected with their village relatives, has grown by six times in the last 10 years (Corral *et al.*, 2015). In addition, poverty decreased between 2003 and 2013 from 45 to 33 % (Corral *et al.*, 2015), with the great majority of the poorest people being concentrated in the Islamic far north where bushmeat consumption is anyway moderate (our unpublished observations). Therefore, the ‘new’ Nigerian middle-class person has been started to perceive the different kinds of bushmeat animals as being interchangeable in the majority of local cooking recipes.

DOES BUSHMEAT TRADE LOCALLY DEplete TARGET SPECIES AND COMMUNITIES?

Although methods of hunting are different and mostly species-specific (Akani *et al.*, 2015b), it is demonstrated that the majority of the harvested species (in either numbers and biomass) are mammals (ungulates and rodents in particular, see Eves & Ruggiero, 2000; Robinson & Bennett, 2000; De Merode *et al.*, 2004; Fa *et al.*, 2005, 2006; Petrozzi *et al.*, 2016), with reptiles, birds, and amphibians being less important (Fa *et al.*, 2006; Taylor *et al.*, 2015; Petrozzi *et al.*, 2016). Longitudinal monitoring of some bushmeat markets revealed changes in the frequency of traded species, likely reflecting changes in species availability and hence depletion for some of them (Holbech, 1998; Rowcliffe *et al.*, 2003; Cowlishaw *et al.*, 2005). It has also been explicitly argued that data on harvested animals can be employed to assess fauna depletion (Crookes *et al.*, 2006). Because of the intensiveness of the trade, mammals seem to be the most likely group of vertebrates to be under immediate threat due to bushmeat trade.

We agree that there is substantial empirical evidence that bushmeat utilization and trade may locally deplete target animal species. For instance, duikers were heavily depleted in Bioko island because of the bushmeat trade (Albrechtsen *et al.*, 2007; Grande-Vega *et al.*, 2016), and in southern Nigeria the population densities of forest tortoises (*Kinixys erosa* and *Kinixys homeana*) were much higher at three forest sites where villagers did not catch them than at three similar sites where villagers actively hunt for them (Luiselli, 2003). In addition, many interviewed hunters reported that the abundance of tortoises remarkably decreased under hunting pressure (Luiselli *et al.*, 2013), with the remnant populations being confined to few mature forest spots even inside wide protected areas (Luiselli *et al.*, 2016). Many other cases may probably arise with further field researches.

WHEN LARGE ANIMALS DISAPPEAR FROM THE MARKETS, DOES IT NECESSARILY MEAN THAT THEIR POPULATIONS WERE MUCH DEPLETED OR EXTIRPATED?

A frequent assumption of the bushmeat literature is that, when in a given market the traded animals are essentially medium-small sized, it would mean that the wildlife population is overexploited (the ‘depletion rule’). In fact when large mammals are heavily harvested and it becomes much more difficult to hunt them, there is a shift of sold animals from preferred marketable large-bodied species with low reproduction rate, to smaller-bodied species with higher rate of reproduction. Overall, this shift has been interpreted as an indication that the harvesting is unsustainable (Fa *et al.*, 2000, 1995, 2005; Wilkie & Carpenter, 1999; Willcox & Nambu, 2007; Poulsen *et al.*, 2009; Nasi *et al.*, 2011; Dupain *et al.*, 2012). Although crucial from a conservation perspective, the ‘depletion rule’ has never been tested with convincing field data. Thus, in our opinion, it is plausible but still remains almost entirely tentative. Empirically, the ‘depletion rule’ is supported by the fact that, in many areas of Africa, small-sized mammals (= rodents) become

important prey items in disturbed areas (Eves & Ruggiero, 2000), where there is a presumably scarce availability of larger species (e.g., antelopes). However, it is our opinion that cultural complications may be inappropriately overlooked by using such an assumption without a critical analysis of the social and ethnic peculiarities of local communities. For instance, in southern Nigeria (and especially in Cross River State), almost all the hunters interviewed by us revealed that they would deliberately select not to hunt for large animals (elephants, gorillas, chimpanzees, buffaloes, etc) because of the existing traditional system of having to share out/deliver several animal parts (meat) of the larger mammals whenever killed to a large section of community members (Eniang *et al.*, 2016). Large game animals, whenever killed by any hunter, have to be declared by hunter who killed it. Tradition demands that the hunter must send several parts of the prey to the eldest persons in his family, irrespective of their place of residence or distance (Eniang *et al.*, 2016). Hunters interviewed on this stuff ($n = 10$ in Cross River State; $n = 23$ in Rivers State; $n = 8$ in Bayelsa State) agreed that they will prefer to kill small to medium sized mammals (like *Cercopithecus* monkeys) and small-medium sized antelopes (*Philantomba* spp.) or big rodents (cane rats) than to kill any mega fauna individual. For them, it is not the lost of valid portions of the meat that hurts most, but the time and money spent to deliver the parts to people who may be living in very distant places. Similar answers were given by 14 independent hunters interviewed by us in Kpalimé and Badou (south-western Togo).

Because the answers given on this stuff by hunters were very similar in such different socio-cultural contexts as Nigeria and Togo, we think that the above-mentioned pattern is likely widespread in West Africa. If indeed the above pattern can be generalized to wide regions of West Africa, the implications can be serious for *a-priori* accepting the ‘depletion rule’. Indeed, the absence of large species in the markets (i) may actually reflect more the active avoidance by hunters than their extirpation from the wild, and (ii) may be linked to the economic structure of the market areas. We predict that, when hunters reside in places where people tend to be sedentary, they are more ready to hunt for large game species than in areas where people emigration rate is high. Thus, in areas where the economy is rapidly growing and rural people tend to emigrate towards cities far away (thus spreading a given family through far distances), hunters will tend to avoid killing of large animals. In these cases, the ‘depletion pattern’ of large animals from markets will appear more likely, independently on whether any depletion has really occurred in the wild. Obviously, we do not mean that the ‘depletion rule’ is always wrong. We just consider very likely that, in economically developed and relatively rich areas (e.g., in southern Nigeria; Corral *et al.*, 2015), large mammals tend to be absent or scarce in markets just because it is not convenient for the hunters to catch them, and not because of their supposed extirpation from the wild. It is advised that, future studies should focus on the cultural correlates of the people inhabiting sites where the ‘depletion rule’ is applied instead of assuming *a priori* its validity.

CONCLUSIONS

Overall, we would like to stress that there is a tendency of bushmeat studies to (i) under-evaluate the cultural flexibility of people involved in the trade and (ii) generalize patterns/explanations also when there is limited scientific evidence of a given phenomenon (e.g., the case of the ‘depletion rule’ presented above). Therefore, we would urge the scientific community to explore in much more detail the heterogeneity of people alimentary preferences and the eventual implications that local cultures and social contexts may have on the flexibility patterns of the bushmeat trade dynamics. We consider as *absolutely essential* that bushmeat trade biologists should:

(1) work in close cooperation with local scientists in order to gather more complete and objective data, as many hunters/traders would not answer freely and show openly the whole of

their sales to foreigners, especially to white people (Knapp *et al.*, 2010; St. John *et al.*, 2010, 2011; Keane *et al.*, 2011; Jenkins *et al.*, 2011; Moro *et al.*, 2013; Nuno *et al.*, 2014).

(2) explore the trade dynamics by organizing a multidisciplinary investigation task, with social scientists, economists, and cultural studies experts actively participating at all phases of data collection and analysis. Long-term studies should also be promoted, given that multiple sources of bias may seriously affect short-term studies on the bushmeat dynamics (McNamara *et al.*, 2015).

More specifically, it would be necessary, for each case of study, to: define a spatially explicit identikit of: (a) the alimentary preferences of consumers in each geographic set (by ethnicity, age, sex, income level, place of residence, and school degree); (b) of the characteristics of bushmeat as a consumable goods with the aim of identifying the properties of this type of consumable goods. For instance, if it is a necessity goods, the bushmeat should have different properties than if it is a luxury goods, but the available studies clearly differ in their view on whether it is a necessity or a luxury goods. Thus, it is very likely that there should be a strong spatial heterogeneity in bushmeat characteristics as a consumable goods. It would also be necessary to define (a) the basket of goods for the bushmeat and the correlated utility curve (each basket of goods being correlated to a precise utility function; see Varian, 1992), and (b) the technical rate of substitution (TRS) between bushmeat and the other goods within each basket of goods (Varian, 1992).

Based on the definition of the above-mentioned points, it would be possible to obtain a reliable picture of the true economic role of bushmeat in the local economies under a strong economical theoretical background (Wilkie & Godoy, 2001; Mankiw, 2009; Schulte-Herbrüggen *et al.*, 2013), and not using the mainly correlational analyses that have been used for most of the conclusions reported so far in the bushmeat trade literature in conservation ecology journals.

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